

RESEARCH OUTPUTS / RÉSULTATS DE RECHERCHE

Biodiversity effects on ecosystem functioning respond unimodally to environmental stress

Baert, Jan; Eisenhauer, Nico; JANSSEN, C.; De Laender, Frédéric

Published in:
Ecology Letters

DOI:
[10.1111/ele.13088](https://doi.org/10.1111/ele.13088)

Publication date:
2018

Document Version
Peer reviewed version

[Link to publication](#)

Citation for pulished version (HARVARD):

Baert, J, Eisenhauer, N, JANSSEN, C & De Laender, F 2018, 'Biodiversity effects on ecosystem functioning respond unimodally to environmental stress', *Ecology Letters*, vol. 21, no. 8, pp. 1191-1199.
<https://doi.org/10.1111/ele.13088>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 Biodiversity effects on ecosystem functioning respond unimodal to
2 environmental stress

3 Baert Jan M.^{1,2*}, Eisenhauer Nico^{3,4}, Janssen Colin R.¹ and De Laender Frederik⁵

4 ¹ Laboratory of Environmental Toxicology and Applied Ecology, Ghent University, Coupure Links
5 653, 9000 Ghent, Belgium

6 ² Ethology (ETHO), University of Antwerp, Universiteitsplein 1, 2610 Antwerp, Belgium

7 ³ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz
8 5e, 04103 Leipzig, Germany

9 ⁴ Institute of Biology, Leipzig University, Deutscher Platz 5e, 04103 Leipzig, Germany

10 ⁵ Institute of Life-Earth-Environment, Namur Institute of Complex Systems, Research Unit of
11 Environmental and Evolutionary Biology, University of Namur, Rue de Bruxelles 61, 5000
12 Namur, Belgium

13 * Corresponding author e: Jan.Baert@UGent.be t: +32 9264 3767

14 **Author contributions**

15 JMB and FDL conceived the idea. JMB implemented the model and analysed the data. JMB, NE, CRJ
16 and FDL contributed to discussions and wrote the manuscript.

18 **Data accessibility statement**

19 References for all studies used in the meta-analyses with detailed descriptions of the source of the
20 data are given in Table S1.

22 **Manuscript info**

23 Type: Letter

24 Abstract: 150 words

25 Text: 4026 words

26 Figures: 4

27 Tables: 1

28 **Abstract**

29 Understanding how biodiversity (B) affects ecosystem functioning (EF) is essential for assessing the
30 consequences of ongoing biodiversity changes. An increasing number of studies, however, shows that
31 environmental conditions affect the shape of BEF relationships. Here, we first use a game-theoretic
32 community model to reveal that a unimodal response of the BEF slope can be expected along
33 environmental stress gradients, but also that the ecological mechanisms underlying this response may
34 vary depending on how stress affects species interactions. Next, we analyzed a global dataset of 44
35 experiments that crossed biodiversity with environmental conditions, confirming our main model
36 predictions: the effect of biodiversity on ecosystem functioning is greater at intermediate levels of
37 environmental stress, but this effect varies considerably among studies depending on the type of
38 species interactions. Together, these results suggest that increases in stress from ongoing global
39 environmental changes may amplify the consequences of future biodiversity changes.

40

41

42

43

44

45

46

47

48

49

50

51

52

53

Introduction

Over the past 25 years, a compelling number of experiments has demonstrated that biodiversity affects ecosystem functioning (Chapin *et al.* 1997; Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2011, 2012). Since most studies support a positive biodiversity-ecosystem functioning (BEF) relationship, this has raised concerns that ecosystem function provisioning is at risk from ongoing global biodiversity changes (Hooper *et al.* 2005, 2012; Cardinale *et al.* 2012). However, evidence is also mounting that the consequences of biodiversity changes may not be predictable from a single, universal BEF relationship (Mittelbach *et al.* 2001; Pärtel *et al.* 2010; Tilman *et al.* 2014). Not only can the shape of BEF relationships differ among ecosystems (Cardinale *et al.* 2011, 2012), an increasing number of studies now demonstrates that changes in environmental conditions can also alter the shape of BEF relationships within a system (Pfisterer & Schmidtke 2002; Wardle & Zackrisson 2005; Li *et al.* 2010; Steudel *et al.* 2011, 2012; Isbell *et al.* 2015; Baert *et al.* 2016; Guerrero-Ramírez *et al.* 2017). How environmental changes alter the shape of the BEF relationship thereby appears to strongly depend on both the system and environmental change driver under study (Cowles *et al.* 2016; Ratcliffe *et al.* 2017). However, few studies have so far explored the processes underlying observed environmental change-induced alterations in BEF relationships (Rixen & Mulder 2005; Baert *et al.* 2016; Hodapp *et al.* 2016). Hence, it remains unstudied if differences among studies in how environmental changes alter BEF relationships can be reconciled within a single mechanistic framework. This is a major knowledge gap as observations and prognoses suggest rapid future changes in environmental conditions to go hand in hand with biodiversity change, which can cause the consequences of predicted biodiversity changes to deviate from the current expectations that are based on the current-day environmental conditions (Pereira *et al.* 2010; Sala *et al.* 2011; Hooper *et al.* 2012; Pimm *et al.* 2014).

Biodiversity research has thus far mostly focused on aggregated ecosystem functions (e.g. total biomass production) in single trophic level systems (Hooper *et al.* 2005; Tilman *et al.* 2014; Ratcliffe *et*

80 *al.* 2017). Such ecosystem functions typically consist of the sum of the individual species' functional
81 contributions. Biodiversity effects on aggregated ecosystem functions therefore result from
82 differences in the relative strength of inter- and intraspecific interactions, which cause species to
83 function differently in the presence of other species (Loreau & Hector 2001; Fox 2005). Two classes of
84 biodiversity effects are thereby discerned: dominance and complementarity effects (Loreau & Hector
85 2001; Fox 2005). Dominance effects refer to changes in ecosystem functions through changes in
86 species' functional contributions as a result of competitive replacement, and hence increase
87 ecosystem functioning when functional and competitive abilities are correlated so that high-
88 functioning species replace low-functioning species. Complementarity effects, in contrast, refer to
89 changes in species functional contributions by alterations in the amount of competition through the
90 presence of heterospecifics, but without resulting in competitive replacement. Niche complementarity
91 and facilitation are hence two important drivers of positive complementarity effects, increasing
92 species' functioning by reducing the amount of competition individuals experience in mixed
93 communities compared to monocultures (Loreau & Hector 2001; Mulder *et al.* 2001; Fox 2005). A
94 distinction can thereby be made between trait-independent and trait-dependent complementarity
95 effects. Trait-independent complementarity effects refer to the average complementarity effect
96 across species as a result of all interactions in the system. Trait-dependent complementarity effects
97 designate how species deviate from this average complementarity effect in relation to their functional
98 traits, generally quantified as their monoculture yield, as a result of asymmetric or one-way
99 interactions. Both classes of biodiversity effects can also be negative. Dominance of species with low
100 functional abilities and antagonistic interactions that increase competition can accordingly result in
101 negative dominance and complementarity effects, respectively, and thus in negative BEF relationships
102 (Loreau & Hector 2001; Fox 2005).

103
104 Theoretically, the environmental dependency of BEF relationships should thus arise from changes in
105 species functional contributions that alter dominance and complementarity effects (Baert *et al.* 2016).

106 Environmental change can affect species functional contributions directly and indirectly. Interspecific
107 differences in species' sensitivities to the environmental changes determine direct effects. Species
108 interactions may cause additional indirect effects by changing the density of a species' competitors
109 (May 1974; Mccann *et al.* 1998; Ives *et al.* 1999). Opposing ecological theories exist, however, on the
110 effect of environmental stress on these species interactions themselves, assuming the per-capita to
111 either remain unaffected, change in strength, or even shift from competitive to facilitation at high
112 stress (Chesson & Huntly 1997; Hart & Marshall 2013). The importance of environmental stress effects
113 on species interactions for biodiversity effects on function remains unresolved at present (Baert *et al.*
114 2016).

115
116 Environmental stress invariably selects for tolerant species. We therefore hypothesize that the slope
117 of BEF relationships should initially increase with environmental stress. Biodiversity increases the
118 probability that a system will contain tolerant species that can replace sensitive species (in line with
119 the insurance effect of biodiversity, Yachi & Loreau 1999). Hence, more diverse systems are less likely
120 to experience severe reductions in function compared to less diverse systems, resulting in an increased
121 slope of BEF relationships (Steudel *et al.* 2012; Hodapp *et al.* 2016). However, the BEF relationship
122 should collapse to a horizontal line when stress is sufficiently high to inhibit the growth of all species.
123 Thus, overall, the slope of a BEF relationship should respond to stress in a unimodal way. Moreover,
124 stress inevitably induces a correlation between functional and competitive abilities, causing tolerant
125 species that grow relatively well in monoculture to displace sensitive species as stress intensifies (Baert
126 *et al.* 2016). Hence, we expect that the response of the dominance effect to stress will be the key driver
127 of this unimodal response.

128
129 Here, we first used a game theoretic competition model to explore how increasing environmental
130 stress alters BEF relationships for aggregated ecosystem functions and the underlying dominance and
131 complementarity effects in competitive systems. We simulated four different scenarios of

environmental stress effects on per-capita interactions: environmental stress had either no effect, increased, or decreased the strength of per-capita interactions without changing the type of species interactions, or reduced per-capita interactions with obligate shifts to complementarity at high levels of environmental stress as postulated by the stress gradient hypothesis (REF). Direct effects of environmental stress on fitness were modelled as reductions in species per-capita growth rates in all scenarios. We tested if BEF-relationships and underlying biodiversity effects responded monotonically or unimodally to increasing environmental stress, by fitting second order polynomials to the simulated data. To assess the generality of our findings, we performed this analysis for a wide range of BEF relationships that are theoretically possible under unstressed conditions, including negative, horizontal, and positive BEF relationships. Next, we confronted model predictions with observed changes in BEF relationships from a meta-analysis of 44 studies in primary producer systems that manipulated species richness under at least 3 different environmental conditions.

Methods

Model structure

We used a stochastic game theoretic community model (Huang *et al.* 2015) to simulate a broad spectrum of theoretically possible BEF relationships. In this model, population dynamics are thereby assumed to be exclusively driven by birth, death, and inter- and intraspecific interaction processes, occurring at rates b , d and a , respectively. For every species i , the rates at which its density (N_i) may increase (T_i^+) or decrease (T_i^-) by one individual can be expressed as:

$$T_i^+ = b_i N_i \quad (\text{eq. 1}),$$

$$T_i^- = d_i N_i + N_i \sum_{j=1}^n a_{i,j} N_j \quad (\text{eq. 2}),$$

where n is the number of species in the community. In the absence of heterospecifics (i.e. $n=1$), the equilibrium density of species i thereby equals $a_{i,i}^{-1} (b_i - d_i)$. Note that, as birth and death events

are independent, stochastic demographic fluctuations will occur around the equilibrium population density in the system (Huang *et al.* 2015).

We consider a one-dimensional environmental gradient (E) along which species functioning is altered through direct effects on the per-capita growth rate (Fig. 1). The species-specific functional response, $r_i(E)$, was modelled by a normalised gamma distribution to restrict values between 0 and 1 (i.e. maximal fitness; Fig. 1):

$$r_i(E) = \left[\frac{E}{\theta_i (k_i - 1)} \right]^{k_i - 1} e^{-\frac{E}{\theta_i} + (k_i - 1)} \quad (\text{eq. 4}).$$

The shape parameter k_i and scale parameter θ_i of the gamma distribution thus determine the width of the environmental niche ($\sim k_i \theta_i^2$) and the optimal environmental conditions ($k_i \theta_i$) at which the maximal per-capita birth rate of species i is attained. We used a gamma distribution to allow for both symmetrical and asymmetrical niches. Note that values for the environmental gradient are hence restricted to positive values.

The per-capita growth rate of each species along the environmental gradients $b_i(E)$ can hence be written as:

$$b_i(E) = b_{0,i} r_i(E) \quad (\text{eq. 3}),$$

where $b_{0,i}$ is the maximal per-capita birth rate of species i at optimal environmental conditions (Fig. 1).

Since optimal conditions and functional responses may differ among species within a system, we quantify the stressfulness of environmental conditions (E) as the stress intensity (SI), which is the average species' fitness reduction at these environmental conditions (Steudel *et al.* 2012):

$$SI(E) = 1 - \sum_{k=1}^m \frac{r_k(E)}{m} \quad (\text{eq. 5}),$$

where m is the number of species within the experiment (see also model simulations). Hence, stress intensity ranged from 0 for on average optimal conditions to 1 for severely stressed conditions (Fig. 1).

We define four scenarios of environmental stress effects on per-capita interactions, representing the main hypotheses commonly postulated (Hart & Marshall 2013). When the type of species interactions is not altered by stress, stress effects on per-capita interactions are modelled as:

$$a_{i,j}(E) = a_{0,i,j} [1 + \beta_i SI(E)]^\gamma \quad (\text{eq. 6}).$$

The species-specific parameter β_i thereby denotes the strength by increasing environmental stress affects per-capita interactions for a given species. The power γ defines whether per capita interactions are unaffected ($\gamma=0$; scenario 1), increase ($\gamma=1$; scenario 2) or decrease ($\gamma=-1$; scenario 4) with increasing stress. For the fourth scenario in which per capita interactions shift to facilitation by environmental stress, i.e. change sign as proposed by the stress gradient hypothesis (Maestre *et al.* 2009), stress effects on per-capita interactions are modelled as:

$$a_{i,j}(E) = a_{0,i,j} [c_i - SI(E)][1 + \beta_i SI(E)]^\gamma \quad (\text{eq. 7}),$$

where the species-specific parameter c_i indicates the stress intensity at which per capita interactions for species i become negative, and thus shift from competition to facilitation.

Along the one-dimensional environmental gradient, the transition rates of a system of n species under given environmental conditions (E) can thus be written as:

$$T_i^+ = b_i(E) N_i \quad (\text{eq. 8}),$$

$$T_i^- = d_i N_i + N_i \sum_{j=1}^n a_{i,j}(E) N_j \quad (\text{eq.9}).$$

Scenarios and parameterisation

We simulated the model for four scenarios of environmental stress on per-capita interactions. In the first scenario, we assumed no effects of environmental stress on per-capita interactions. Hence, the parameter γ was set to zero for those model simulations (eq. 6). In the second and third scenario, we assumed a continuous increase or decrease in per-capita interactions, and thus competition, but without changes in the type of interactions at high stress (eq. 6). In both scenarios, β_i was sampled from $U(0, 10)$ for each model simulation. The parameter γ was set to 1 (scenario 2) or -1 (scenario 3)

to simulate a continuous increase or decrease strength of per-capita interactions, respectively. In the fourth scenario, we assumed a linear decrease in per-capita interactions with shifts to facilitation at high levels of environmental stress (eq. 7). Identical to scenario 3, β_i was sampled from $U(0, 10)$ and γ was set to -1. The additional parameter c_i , denoting the stress intensity at which per-capita interactions shift from positive to negative, was sampled from $U(0.75, 1)$ for each model simulation.

We used a Monte-Carlo simulation procedure to generate 100 BEF relationships, and simulated changes in each of those BEF relationships by increasing environmental stress, for each of the four scenarios of environmental stress effects on per-capita interactions. The generated set of BEF relationships represented an exhaustive set of ecologically relevant BEF relationships under unstressed conditions, ranging from negative to strongly positive relationships (Fig. 2). Per capita birth rates under optimal conditions, $b_{0,i}$, and per capita mortality rates, d_i , were randomly sampled from $U(0, 1)$ and $U(0, 0.01b_{0,i})$, respectively. The means of the gamma distributions (i.e. the optimal environmental conditions for every species), were sampled from $U(95, 105)$, and the variances were sampled from $U(10, 50)$. The strength of intraspecific interactions a_{ii} , which is the main determinant of differences among species monoculture yields, was sampled from $U(10^{-4}, 10^{-3})$. The strength of interspecific interactions was subsequently sampled from $U(-0.01 a_{ii}, 2 a_{ii})$. A sensitivity analysis of the parameters distributions revealed that the model results did not depend on the parameter distributions: using different sets of ecologically relevant parameter distributions did not alter our results (Fig. S1).

Model simulations

For each simulation, we first generated a pool of 20 species by randomly drawing values for $b_{0,i}$, k_i , θ_i , d_i , α_{ij} and α_{ji} for all species (Fig. S2). Next, 10 communities of 2, 4, 8, and 16 species were randomly assembled from this species pool, representing a standard design used in BEF studies). Community dynamics were then simulated under unstressed conditions and under nine conditions of environmental stress intensity (SI=0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9; Fig. S2). Community dynamics

were simulated using the Gillespie algorithm to shorten simulation times by optimizing the length of the time-steps used (Gillespie 1976). Initial ($t=0$) densities were set to 100 for all species. Population densities always reached their stationary distribution at $t \leq 30$. Simulations were run till $t=50$. Mean species densities were calculated from the species densities between $t=40$ and $t=50$. Each simulation was reiterated 12 times to ensure convergence of the stationary distribution (Fig. S3).

Ecosystem functioning was calculated as the sum of the mean species' densities. BEF relationships at each level of environmental stress were subsequently calculated by linearly regressing functioning against the initial species richness of the system. Biodiversity effects for all environmental conditions were calculated according to the additive partitioning approach by Fox (Fox 2005):

$$\Delta Y = \sum_i^n Y_{o,i} - Y_{e,i} = \sum_i^n (RY_{o,i} - RY_{e,i}) M_i = n \operatorname{cov} \left(\frac{RY_{o,i}}{RYT} - RY_{e,i}, M_i \right) + \operatorname{cov} \left(RY_{o,i} - \frac{RY_{o,i}}{RYT}, M_i \right) + n E(\Delta RY) E(M) \text{ (eq.10),}$$

where ΔY is the deviation between the expected and observed yield, which is the sum of the individual species deviations between observed ($Y_{o,i}$) and expected yields ($Y_{e,i}$). RY denotes the relative yield, i.e. the fraction of the monoculture yield. The expected relative yield ($RY_{e,i}$) thereby equals the species initial proportion in the mixture (i.e. n^{-1}), whereas the observed relative yield is the mean value of each species stationary distribution divided by its monoculture yield under the same environmental conditions ($M_i = a_{i,i} [b_i(Env) - d_i]$). RYT is the relative yield total (i.e. $\sum_i^n RY_{o,i}$).

Review of literature data

We searched Thomas Reuters Web of Knowledge (www.webofknowledge.com) and Google Scholar (www.scholar.google.com) in February 2018 for experiments that manipulated species richness under at least three environmental conditions. We used the search terms "biodiversity", "ecosystem", "function", "productivity", "stress", "temperature", "nutrient", "precipitation", "chemical", "salinity", "environment" in various combinations. We additionally checked the cited literature for further original studies. Data were available as text, excel files or were digitized from the figures in the original

258 publications. Digitized data did not differ by more than 1% among different applications (e.g. Engauge,
259 WebPlot, ExtractGraph digitizer). When slopes and intercepts of BEF relationships were not reported,
260 these were calculated from the data. Only studies that manipulated biodiversity under at least three
261 environmental conditions, and reported the species monoculture functions for all environmental
262 conditions were considered, as this is a prerequisite to calculate the intensity of environmental stress
263 and discriminate between monotonic and unimodal changes in BEF relationships (see Data
264 normalisation and analysis). This yielded a total of 44 studies (Fig. S4, Table S1), all of which used
265 primary producer systems. Environmental gradients comprised drought (n=37), temperature (n=3),
266 pollutants (n=2), salt (n=1), nutrients (n=1) and shade (n=1).

267

268 **Data normalisation**

269 Literature and simulated data were normalized prior to analysis. The severity of the environmental
270 stress was calculated, analogous to model simulations (eq. 5), as the ratio between the average
271 observed monoculture under stress and unstressed conditions for all species in the study. Unstressed
272 conditions were defined as those environmental conditions under which species attained the highest
273 mean monoculture functions. Since the units in which aggregated ecosystem functions are measured
274 varied among studies, slopes were normalized by dividing the linear regression coefficient of the BEF
275 relationship by the average monoculture function under unstressed conditions. Thus, normalised
276 slopes all had species⁻¹ as a unit.

277

278 **Analysis of simulated and empirical data**

279 We carried out the same analyses on the simulated data (including all four scenarios of environmental
280 effects on per-capita interactions) as on the empirical data. First, we tested how the slope of BEF
281 relationships changed along environmental stress gradients using second order polynomials. Next, we
282 tested how the effect on the BEF slope varied among the range of unstressed BEF relationships
283 considered by the model or present in the empirical data. To do so, we regressed the slope under

284 unstressed conditions against the stress intensity at which the BEF slope peaked. The dataset ID (i.e.
285 simulated scenario 1, 2, 3, and 4? or empirical data) was included as an additional factorial fixed effect
286 in the linear regression model to be able to compare among simulated scenarios and between
287 simulations and empirical data. Residual diagnostics were assessed for deviations from normality and
288 homoscedasticity (Fig. S5).

289

290 **Results**

291 **Model simulations**

292 Model simulations revealed highly consistent changes in the slope of BEF relationships, irrespective of
293 how environmental stress affected per-capita interactions (Fig. 2). In all four scenarios, most
294 simulations confirmed a unimodal response of the slope of the BEF relationship to increasing
295 environmental stress: biodiversity effects peaked at intermediate levels of environmental stress (Fig.
296 2). Only when initial BEF slopes were high, the model predicted a monotonic decrease in BEF
297 relationships. When synthesising across the wide range of BEF relationships under unstressed
298 conditions considered by our modelling, we found a negative relationship between the slope under
299 unstressed conditions and the level of environmental stress where the BEF slope peaks (Fig. 2).

300

301 While BEF relationships responded consistently to environmental stress across all simulations, the
302 responses of the underlying biodiversity effects, however, depended strongly on how per-capita
303 interactions were affected by environmental stress. In all four scenarios, environmental stress-induced
304 changes in dominance effects drove the change in BEF relationships (Fig. 3). Unimodal changes in the
305 complementarity effects, in contrast, only contributed to overall changes of the BEF relationship in
306 scenarios 3 and 4, where the strength of per-capita interactions decreased with increasing
307 environmental stress. When per-capita interactions remained constant or increased with
308 environmental stress, complementarity effects instead on average decreased monotonically.

309

Meta-analysis of biodiversity experiments

Observed responses of the slope of BEF relationships to environmental stress, as reported in the 44 empirical studies, confirm predictions of a predominantly unimodal model response of BEF relationships to increasing environmental stress (Fig. 4). In the majority of these studies, fitted polynomials peaked at intermediate levels of environmental stress, while monotonically decreasing polynomials were only supported for studies where BEF slopes in unstressed conditions were strongly positive. Confirming model predictions, the environmental stress intensity where biodiversity effects peaked were indeed negatively related to the slope of the BEF-relationship under unstressed conditions (Fig. 4). This negative relationship was comparable between the simulated and empirical data for all the tested scenarios, and did not significantly differ between the simulated and empirical data for scenarios 3 and 4 (per-capita interactions decreased with increasing stress, Table 1).

Discussion

Our results demonstrate that environmental stress changes biodiversity effects on ecosystem functioning, and that the strength of these changes may vary considerably, yet predictably, among systems. We presented a model that, based on a minimal set of mechanisms, disentangles a general response driven by stress effects on dominance, from system-specific effects resulting from stress effects on complementarity (Fig. 2 and 3). While dominance effects and the BEF slope tend to respond in a unimodal way to increasing environmental stress, the response of complementarity effects to stress strongly depends on the per-capita species interactions and how these are affected by environmental stress (Fig. 3). Our meta-analysis of current biodiversity experiments confirms a key model prediction: the consequences of biodiversity changes for ecosystem functioning are likely to increase at low to intermediate levels of environmental stress (Fig. 4).

Model simulations suggest that the unimodal change in the BEF relationship to increasing environmental stress is primarily driven by species differences in sensitivity to environmental stress

336 through shifts of the dominance effect. As postulated, positive dominance effects are promoted by
337 increasing fitness differences under increasing environmental stress, as species experiencing smaller
338 fitness reductions will increasingly replace species experiencing severe fitness reductions. However,
339 when levels of environmental stress become so high that fitness of most species is severely reduced,
340 the strength of the dominance effect and the slope of the BEF relationship decrease again, because
341 the potential for functional replacement is lost, even in more diverse systems. From this threshold
342 stress level onward, the slope of the BEF relationship decreases until it reaches a flat line at extreme
343 levels of environmental stress, where the functioning of all species is inhibited (Fig. 2). However, when
344 dominant high-functioning species are also most sensitive to environmental stress, increasing stress
345 will replace these with low-functioning species, causing loss of function. This will cause dominance
346 effects to monotonically decrease with increasing environmental stress (Fig. 3).

347
348 Unlike the dominance effect, changes in complementarity effects are more system-specific and vary
349 with the strength of, and environmental effects on, species interactions. Changes in complementarity
350 effects strongly differ among model scenarios. Along an environmental stress gradient, the number of
351 species that can significantly contribute to ecosystem functions is progressively reduced, which
352 decreases the ratio between inter- and intraspecific interactions experienced by the remaining species.
353 When per-capita interactions remain constant, this will reduce both positive and negative
354 complementarity effects at these elevated stress levels. This results in a decrease of complementarity
355 effects along an environmental stress gradient (Fig. 3).

356
357 When environmental stress increases the strength of per-capita interactions, i.e. increases
358 interspecific competition, complementarity effects are likely to decrease even faster with increasing
359 stress. This is because, in this case, stress additionally reduces the potential for positive
360 complementarity effects. Although changes in complementarity effects do not match the overall
361 changes in BEF relationships in both scenarios, per-capita interactions can have a profound effect on

the environmental stress level at which biodiversity effects peak. The slope of the BEF relationship can only increase as long as decreases in complementarity effects are offset by larger increases in dominance effects. Maximal biodiversity effects can therefore be expected to be attained at lower levels of environmental stress when systems are driven by highly positive complementarity effects under unstressed conditions (Fig. 3).

If the strength of per-capita interactions decreases with increasing stress, the reduction in competition can in contrast counteract negative direct effects of environmental stress by increasing complementarity effects under stress. Higher diversity thereby increases the potential for positive complementarity effects, increasing the slope of the BEF relationship, which is even higher when interactions become positive under high environmental stress. However, identical to dominance effects, extreme stress levels will cause direct effects on fitness that are so high that complementarity effects and BEF relationships start to decrease to reach a flat line (Fig. 2 and 3). In all four scenarios, the responses of trait-dependent complementarity effects are similar to those of trait-independent complementarity effects. This can be expected as both are driven by the same mechanisms and only express the extent by which complementarity effects are (a)symmetrical across all species in the system. Only their relative contribution to changes in BEF relationships is highly community-specific and depends on the asymmetry of the species interactions within the system (Fox 2005).

Our results reveal that separating a general from a system-specific response over an environmental gradient will be an important step in reconciling the apparent contradictions among the results reported by experiments manipulating biodiversity under different environmental conditions (ADD SOME CITATIONS+citation to recent forest paper by Lander?). While biodiversity experiments conducted over the past decades almost unequivocally yielded positive relationships (Hooper *et al.* 2005; Cardinale *et al.* 2012), changing environmental conditions have resulted in either increases (refs), decreases (refs), or no effects on the slope of the BEF relationship (refs). The theory presented

388 in the present study allows these results to be interpreted within a single generalised framework,
389 reflecting different system-specific realisations of a unimodal response of BEF relationships to
390 environmental stress gradients. Monotonically decreasing relationships in both simulated and
391 empirical data may thereby in fact represent unimodal relationships that peak at extremely low levels
392 of environmental stress, but which remained undetected by a too coarse resolution of the
393 environmental gradient. Still, only few studies to date have manipulated species richness under a
394 sufficiently broad range of environmental conditions to reveal such a unimodal response (Fig. 4 and
395 S4) as many studies apply only two or three environmental stress levels.

396
397 Our model simulations revealed that shifts in per-capita interactions have important consequences for
398 the mechanisms that can drive shifts in BEF relationships across environmental gradients. Increased
399 niche complementarity and facilitation under environmental stress have been documented to increase
400 in several plant systems (Rixen & Mulder 2005; Maestre *et al.* 2010; Hart & Marshall 2013). Hence, this
401 may explain why the empirical relationship between the slope under unstressed conditions and the
402 stress intensity under which maximal biodiversity effects were attained best corresponded to the
403 model scenarios under which per-capita interactions and competition decreased with increasing stress
404 (Table 1, Fig. 4). Still, only few studies have assessed the biodiversity effects underlying BEF
405 relationships at different environmental conditions (De Boeck *et al.* 2008; Li *et al.* 2010; Steudel *et al.*
406 2011; Baert *et al.* 2016). As such, little empirical support exists for whether changes in BEF relationships
407 are merely driven by dominance effects, or by a combination of dominance and complementarity
408 effects. In addition, it should be noted that throughout this study we have focussed on equilibrium
409 conditions. Environmental stress was assumed to affect species functional contributions through the
410 per-capita growth rate, which caused the system to respond fast to any environmental change. In
411 primary producer systems, environmental stress can affect both somatic growth and reproduction
412 (Ref). As produced seeds generally only germinate in the following growth season, species turnover
413 can be much slower in real systems compared to our model simulations, and may lead to a reduced

importance of shifts in dominance in real systems compared to our model simulations. Finally, in this study, we have restricted our model to first order species interactions. Although there is a growing awareness that higher-order (including multi-trophic) interactions may significantly contribute to ecosystem functions (Soliveres *et al.* 2016; Grilli *et al.* 2017; Barnes *et al.* 2018; Wang & Brose 2018), we focussed on aggregated ecosystem functions within a single trophic level throughout this study. While this might be an oversimplification of real ecosystems, this approach enabled the integration of a maximal number of experimental studies, since most considered single trophic level systems. Our findings reveal that major patterns in primary producer systems, changes in the BEF relationship and underlying biodiversity effects primarily depend on, and can be predicted from, interactions within this single trophic level.

Environmental and biodiversity changes pose major threats to ecosystems worldwide (Hooper *et al.* 2012). Understanding how both processes are intertwined is therefore a major challenge to appropriately assess the consequences of ongoing and future biodiversity changes (Isbell *et al.* 2013, 2015; De Laender *et al.* 2016). The presented results provide a theoretical framework to meet this challenge, as they allow predicting the context-dependence of BEF relationships. Our model simulations revealed testable hypotheses on a consistent change in BEF relationships in response to environmental stress, but also on how the underlying mechanisms and differences in the magnitude of changes in BEF relationships may differ between systems based on differences in the strength and environmental response of per-capita interactions. Moreover, while underlying mechanisms may be strongly system-dependent, our results suggest that the joint effects of forecasted biodiversity and environmental changes are likely to cause greater effects on ecosystem functions than previously anticipated.

Acknowledgments

JMB is indebted to the Research Foundation Flanders (FWO) for his PhD research fellow grant

(B/12958/01). NE acknowledges funding by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (Deutsche Forschungsgemeinschaft, DFG FZT 118) and by the Deutsche Forschungsgemeinschaft to the Jena Experiment (DFG FOR 1451). FDL is indebted to the University of Namur (FSR Impulsionnel 48454E1). The computational resources (Stevin Supercomputer Infrastructure) and services used in this work were provided by the VSC (Flemish Supercomputer Center), funded by Ghent University, the Hercules Foundation and the Flemish Government – department EWI.

References

- Baert, J.M., Janssen, C.R., Sabbe, K. & De Laender, F. (2016). Per capita interactions and stress tolerance drive stress-induced changes in biodiversity effects on ecosystem functions. *Nat. Commun.*, 7, 12486.
- Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., *et al.* (2018). Energy Flux: The Link between Multitrophic Biodiversity and Ecosystem Functioning. *Trends Ecol. Evol.*
- De Boeck, H.J., Lemmens, C.M.H.M., Zavalloni, C., Gielen, B., Malchair, S., Carnol, M., *et al.* (2008). Biomass production in experimental grasslands of different species richness during three years of climate warming. *Biogeosciences*, 5, 585–594.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.
- Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., *et al.* (2011). The functional role of producer diversity in ecosystems. *Am. J. Bot.*, 98, 572–592.
- Chapin III, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., *et al.* (1997). Biotic Control over the Functioning of Ecosystems. *Science (80-.)*, 277, 500–504.
- Chesson, P. & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.*, 150, 519–553.
- Cowles, J.M., Wragg, P.D., Wright, A.J., Powers, J.S. & Tilman, D. (2016). Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Glob. Chang. Biol.*, 22, 741–749.
- Fox, J.W. (2005). Interpreting the “selection effect” of biodiversity on ecosystem function. *Ecol. Lett.*, 8, 846–856.
- Gillespie, D.T. (1976). A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. *J. Comput. Phys.*, 22, 403–434.
- Grilli, J., Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2017). Higher-order interactions stabilize dynamics in competitive network models. *Nature*, 548, 210–213.
- Guerrero-Ramírez, N.R., Craven, D., Reich, P.B., Ewel, J.J., Isbell, F., Koricheva, J., *et al.* (2017). Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nat. Ecol. Evol.*, 1, 1639–1642.

476 Hart, S.P. & Marshall, D.J. (2013). Environmental stress, facilitation, competition, and coexistence. *Ecology*, 94,
477 2719–2731.

478 Hodapp, D., Hillebrand, H., Blasius, B. & Ryabov, A.B. (2016). Environmental and trait variability constrain
479 community structure and the biodiversity- productivity relationship. *Ecology*, 97, 1463–1474.

480 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B. a, Matulich, K.L., *et al.* (2012). A global
481 synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105–8.

482 Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). Effects of biodiversity
483 on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

484 Huang, W., Hauert, C. & Traulsen, A. (2015). Stochastic game dynamics under demogrpahic fluctuations. *Proc.*
485 *Natl. Acad. Sci. U. S. A.*, 112, 9064–9069.

486 Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., *et al.* (2015). Biodiversity increases
487 the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.

488 Isbell, F., Reich, P.B., Tilman, D., Hobbie, S.E., Polasky, S. & Binder, S. (2013). Nutrient enrichment, biodiversity
489 loss, and consequent declines in ecosystem productivity. *Proc. Natl. Acad. Sci. U. S. A.*, 110, 11911–6.

490 Ives, A.R., Gross, K. & Klug, J.L. (1999). Stability and Variability in Competitive Communities. *Science (80-)*,
491 286, 542–544.

492 De Laender, F., Rohr, J.R., Ashauer, R., Baird, D.J., Berger, U., Eisenhauer, N., *et al.* (2016). Re-introducing
493 environmental change drivers in biodiversity-ecosystem functioning research. *Trends Ecol. Evol. Evol.*, 31,
494 905–915.

495 Li, J.-T., Duan, H.-N., Li, S.-P., Kuang, J.-L., Zeng, Y. & Shu, W.-S. (2010). Cadmium pollution triggers a positive
496 biodiversity-productivity relationship: evidence from a laboratory microcosm experiment. *J. Appl. Ecol.*,
497 47, 890–898.

498 Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments.
499 *Nature*, 412, 72–76.

500 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., *et al.* (2001). Biodiversity and
501 ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.

502 Maestre, F.T., Bowker, M. a, Escobar, C., Puche, M.D., Soliveres, S., Maltez-Mouro, S., *et al.* (2010). Do biotic
503 interactions modulate ecosystem functioning along stress gradients? Insights from semi-arid plant and
504 biological soil crust communities. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 365, 2057–2070.

505 Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009). Refining the stress-gradient hypothesis for
506 competition and facilitation in plant communities. *J. Ecol.*, 97, 199–205.

507 May, R.M. (1974). *Stability and complexity in model ecosystems*. Princeton University Press, Princeton.

508 Mccann, K., Hastings, A. & Huxel, G.R. (1998). Weak trophic interactions and the balance of nature. *Nature*,
509 395, 794–798.

510 Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., *et al.* (2001). What is the
511 observed relationship between species richness and productivity? *Ecology*, 82, 2381–2396.

512 Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001). Physical stress and diversity-productivity relationships: the
513 role of positive interactions. *Proc. Natl. Acad. Sci. U. S. A.*, 98, 6704–6708.

514 Pärtel, M., Zobel, K., Laanisto, L., Szava-Kovats, R. & Zobel, M. (2010). The productivity - Diversity relationship:
515 Varying aims and approaches. *Ecology*, 91, 2565–2567.

516 Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., *et al.*
517 (2010). Scenarios for global biodiversity in the 21st century. *Science (80-)*, 330, 1496–1501.

518 Pfisterer, A.B. & Schmidtko, A. (2002). Diversity-dependent production can decrease the stability of ecosystem
519 functioning. *Nature*, 416, 84–86.

520 Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., *et al.* (2014). The biodiversity of
521 species and their rates of extinction, distribution, and protection. *Science (80-)*, 344, 987.

522 Ratcliffe, R., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., *et al.* (2017). Biodiversity
523 and ecosystem functioning relations in European forests depend on environmental context. *Ecol. Lett.*,
524 20, 1414–1426.

525 Rixen, C. & Mulder, C.P.H. (2005). Improved water retention links high species richness with increased
526 productivity in arctic tundra moss communities. *Oecologia*, 146, 287–299.

527 Sala, O.E., Sala, O.E., Chapin, S.F., Armesto, J.J., Berlow, E., Bloomfield, J., *et al.* (2011). Global Biodiversity
528 Scenarios for the Year 2100. *Science (80-.)*, 287, 1770–1775.

529 Soliveres, S., Van Der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., *et al.* (2016). Biodiversity at
530 multiple trophic levels is needed for ecosystem multifunctionality. *Nature*, 536, 456–459.

531 Steudel, B., Hautier, Y., Hector, A. & Kessler, M. (2011). Diverse marsh plant communities are more consistently
532 productive across a range of different environmental conditions through functional complementarity. *J.*
533 *Appl. Ecol.*, 48, 1117–1124.

534 Steudel, B., Hector, A., Friedl, T., Löffke, C., Lorenz, M., Wesche, M., *et al.* (2012). Biodiversity effects on
535 ecosystem functioning change along environmental stress gradients. *Ecol. Lett.*, 15, 1397–1405.

536 Tilman, D. & Downing, J.A. (1994). Diversity and stability in grasslands. *Nature*, 367, 363–365.

537 Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and Ecosystem Functioning. *Annu. Rev. Ecol. Evol. Syst.*,
538 45, 41–493.

539 Wang, S. & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: the vertical diversity
540 hypothesis. *Ecol. Lett.*, 21, 9–20.

541 Wardle, D. a & Zackrisson, O. (2005). Effects of species and functional group loss on island ecosystem
542 properties. *Nature*, 435, 806–810.

543 Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment : The
544 insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.*, 96, 1463–1468.

547

548

549 **Figures**

550

551

552

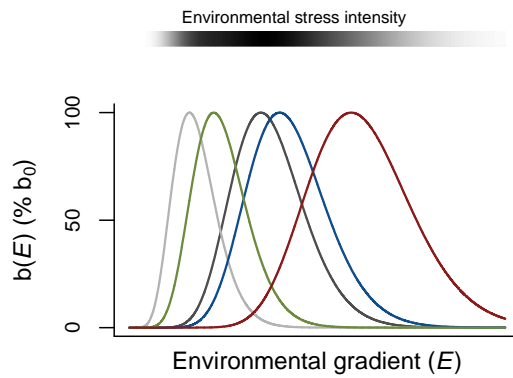


Fig. 1. Species functional responses and definition of environmental stress as assumed in the model. Niches of five hypothetical species are depicted as the change in the per-capita birth rate (b) over an environmental gradient (E). Note that values have been normalised to the percentage reduction in the maximal per-capita birth rate, $b_{i,0}$. The stress intensity of an environmental condition is calculated as the average % reduction in the maximal per capita birth rate of the species. Lighter colours indicate higher environmental stress intensity.

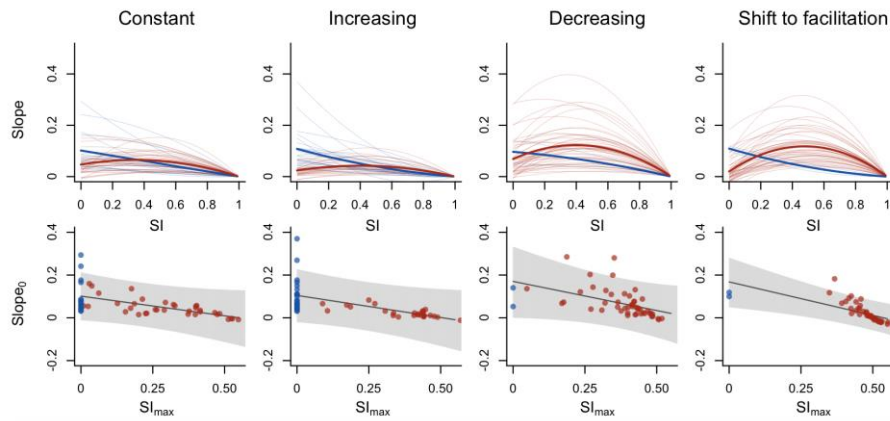


Fig. 2: Upper panels: simulated changes in slopes of BEF relationships with increasing environmental stress intensity (SI) for constant, increasing, decreasing, and shifts from competitive to facilitative per-capita interactions under increasing environmental stress intensity. Lower panels: simulated relationship between the slope of the BEF relationship under unstressed environmental conditions ($Slope_0$) and the stress intensity at which a maximal slope is attained (SI_{max}). Red lines and dots indicate unimodal relationships, blue lines and dots indicate monotonic relationships. Thick lines represent the model predictions for unimodal and monotonic relationships. The grey shaded area corresponds to the 95% prediction interval.

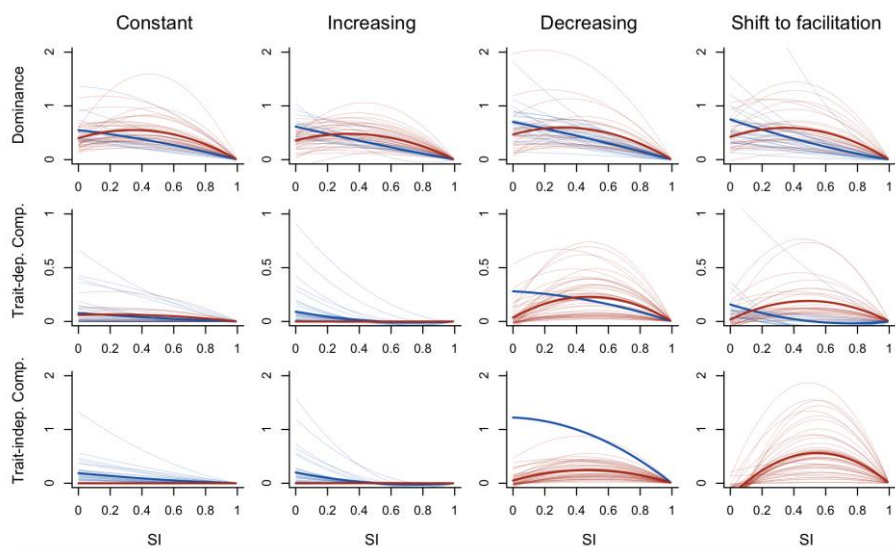


Fig. 3: Simulated changes in dominance, trait-dependent and trait-independent complementarity effects with increasing environmental stress intensity (SI) for constant, increasing and decreasing per-capita interactions under increasing environmental stress intensity. Red lines indicate unimodal relationships, blue lines indicate monotonic relationships. Thick lines represent the mean model predictions for unimodal and monotonic relationships.

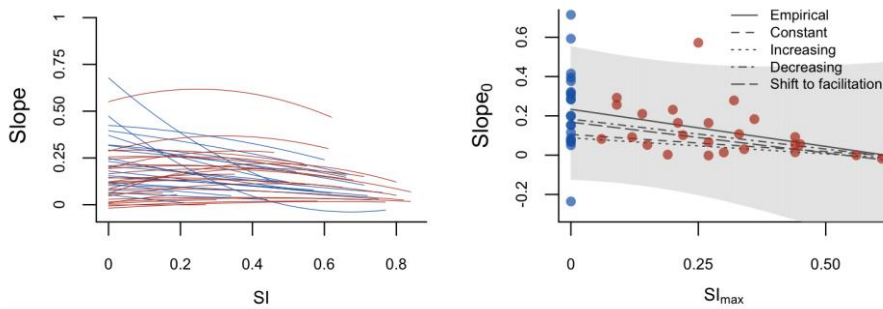


Fig. 4: Left panel: Empirical observed changes in slopes of BEF relationships with increasing environmental stress intensity (SI). Right panel: Empirical and modelled relationship between the slope of the BEF relationship under unstressed environmental conditions ($Slope_0$) and the stress intensity at which a maximal slope is attained (SI_{max}). Red lines and dots indicate unimodal empirical relationships, blue lines and dots monotonic empirical relationships for the empirical data. The grey shaded area corresponds to the 95% prediction interval for the empirical data.

Tables

620 **Table 1:** Estimated relationship between the the slope under unstressed conditions and the stress
621 intensity at which maximal biodiversity effects are attained. Significances for model simulations are
622 expressed against the value of the empirical regression.

	Estimate	p-value
Intercept empirical data	0.233	<0.001
Intercept constant interactions	0.105	<0.001
Intercept increasing interactions	0.087	<0.001
Intercept decreasing interactions	0.183	0.136
Intercept shift to facilitation	0.165	0.314
SI _{max} empirical data	-0.379	<0.001
SI _{max} constant interactions	-0.174	<0.001
SI _{max} increasing interactions	-0.163	<0.001
SI _{max} decreasing interactions	-0.305	0.38
SI _{max} Shift to facilitation	-0.311	0.68

623
624
625